Barrier effects on vertebrate distribution caused by a motorway crossing through fragmented forest landscape

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Abstract
Barrier effects on vertebrate distribution caused by a motorway crossing through fragmented forest landscape.— We analysed the effects of a 25–year–old motorway on the distribution of five vertebrates inhabiting a fragmented forest landscape and differing in their ability to move across linear infrastructures. We found clear evidence of barrier effects on the distribution of the forest lizard *Psammodromus algirus*. The roe deer (*Capreolus capreolus*) was also unequally distributed on both sides of the motorway, but this could also be due, at least in part, to fragmentation. The eyed lizard (*Timon lepidus*), that can move through open fields, showed no evidence of barrier effects. The distribution of two small birds (*Erithacus rubecula* and *Phylloscopus bonelli*) was unaffected by the motorway. Our results show that a motorway may severely restrict the distribution of species which can withstand high levels of forest fragmentation but show limited dispersal ability, highlighting the role of linear infrastructures in shaping species' ranges at regional scales.

Key words: Abundance patterns, Barrier effect, Dispersive ability, Lizard, Road ecology, Roe deer.

Resumen
Efecto barrera en la distribución de vertebrados causada por las autovías que cruzan un paisaje forestal fragmentado.— En este trabajo se analizan los efectos de una autovía construida hace 25 años sobre la distribución en un paisaje forestal fragmentado de cinco vertebrados que difieren en su capacidad de atravesar infraestructuras lineales. Se encontraron evidencias de efecto barrera en la distribución de la lagartija colilarga *Psammodromus algirus*. El corzo (*Capreolus capreolus*) presentó una distribución desigual a ambos lados de la carretera, aunque también atribuible, al menos en parte, a diferencias en el grado de fragmentación. El lagarto ocelado (*Timon lepidus*), que puede moverse a través de los cultivos, no mostró ninguna evidencia de efecto barrera. La distribución de dos pequeños paseriformes (*Erithacus rubecula* y *Phylloscopus bonelli*) no se vió afectada por la autovía. Estos resultados demuestran que una autovía puede restringir la distribución de especies capaces de soportar altos niveles de fragmentación del paisaje pero con escasa capacidad de dispersión, poniendo de manifiesto el efecto potencial de las infraestructuras lineales sobre la distribución de las especies a escala regional.

Palabras clave: Patrones de abundancia, Efecto barrera, Capacidad de dispersión, Lagartijas, Ecología de las carreteras, Corzo.

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Introduction

Barrier effects of linear infrastructures may have different origins, such as occupation of natural dispersal pathways of populations, neo–phobic behaviour of individuals (which may alter dispersal patterns), or physical isolation caused by fences that run alongside roads and railways to prevent collision. As a consequence, linear infrastructures usually divide animal populations into sub–populations that may become isolated, thereby compromising their long–term persistence (Forman & Alexander, 1998; Trombulak & Frissell, 2000).

Many studies have assessed the effectiveness of management actions to correct the barrier effect, such as building overpasses, underpasses or culverts to favour dispersal (Clevenger & Waltho, 2005; Grilo et al., 2008; Mader, 1984; Mata et al., 2005). Other studies have emphasized the need to determine the effects of interrupted gene flow between populations separated by linear infrastructures (*e.g.* Epps et al., 2005; Riley et al., 2006; Strasburg, 2006). However, less effort has been devoted to study the impact of linear infrastructures on the regional distribution of species (Baguette & Van Dyck, 2007; Roedenbeck et al., 2007; Underhill & Angold, 2000).

Ranges of local species may undergo different dynamics on either side of a linear infrastructure when the barrier disconnects marginal sectors from core areas in the regional distribution of each species (Taylor et al., 1993). In these circumstances, the barrier effect will decrease the ability of local populations to avoid extinction through the rescue effect due to individuals coming from source areas (Brown & Kodric–Brown, 1977; Goodwin & Fahrig, 2002). Reduced connectivity may promote independent population trends on either side of the linear infrastructure. These trends are typically mediated by asymmetric source–sink dynamics that may eventually cause local extinctions in isolated habitat patches (Pulliam, 1988; Taylor et al., 1993, Shepard et al., 2008).

We studied the effect of a motorway on the distribution of several forest species in a fragmented landscape in northern Spain (fig. 1). The forest patches in this area become scarcer and increasingly fragmented westwards. The motorway runs perpendicular to the westernmost tips of this fragmented area, isolating them from eastern habitat patches. These eastern habitat patches are better connected to large forests located further east in the 'Sierra de la Demanda' mountain range, and might act as source habitats. When the motorway was constructed 25 years ago, populations of forest vertebrates were expanding westwards from these mountains as a consequence of human abandonment of low productivity highlands (Sáez–Royuela & Tellería, 1986; Tellería & Sáez–Royuela, 1984). A barrier effect might therefore have caused asymmetric population dynamics on either side of the motorway, obstructing the recovery of local extinctions in western forest patches by individuals moving from mountain forests.

Our aim was to assess whether there is any evidence of this barrier effect two and a half decades after the construction of this infrastructure. If the motorway is a barrier against the dispersal of a species, we could expect different patterns of habitat occupancy and abundance on either side of the road, with reduced patch occupancy and/or abundance on the western side of the motorway. We can also expect asymmetric distribution of species with different susceptibility to barrier effects (Fahrig & Rytwinski, 2009). To identify such differences, we analysed the distribution of five vertebrate model species: a large mammal (the roe deer *Capreolus capreolus*), two small birds (the European robin *Erithacus rubecula* and the Bonelli's warbler *Phylloscopus bonelli*), and two lacertid lizards (the eyed lizard *Timon lepidus* and the large psammodromus *Psammodromus algirus*). In principle, the motorway should not represent a barrier against dispersal of birds as they can fly over it.

Material and methods

Study area

We studied the distribution of the selected species in an agricultural landscape located around Lerma, northern Spain (fig.1). In this area, forests cover ca. 10% of their former range and are dominated by evergreen Holm Oaks *Quercus ilex* and deciduous oaks *Q. pyrenaica* and *Q. faginea* (Díaz et al., 2005).

The distribution of forest vertebrates in this fragmented landscape has been studied by the authors since the mid–1980s, when the highway A–1 (E–50 according to European nomenclature) was built to substitute an unfenced, single carriageway road (N–1). The motorway, which opened to traffic in 1985, is a dual–carriageway protected by fences throughout its length. It is one of the main transportation highways to connect Spain, Portugal and the Maghreb countries with the rest of Europe.

We studied animal distributions in forest remnants located on either side of the motorway between Gumiel de Izán (41º 46' 24'' N, 3º 41' 17'' W; 854 m a.s.l.) and Saldaña de Burgos (42º 15' 34'' N, 3º 41' 48'' W; 863 m a.s.l.; fig. 1). The study area represents 40 km of the road, which are crossed by 27 culverts (0.7/km), 24 overpasses (0.6/km), and 29 underpasses (0.7/km) that may potentially be used by several vertebrates (Mata et al., 2005), meaning an average of 2 passes/km. The frequency of passes meets the Spanish regulation (Ministerio de Medio Ambiente, 2006) aimed to favour dispersal of large mammals (0.3–1 passes/km) and small vertebrates (1–2 passes/km). A 4–km long segment crossing forested landscape to the north of Lerma (fig. 1) is critical for forest vertebrates to cross from one side of the motorway to the other. This segment is crossed by one overpass and five underpasses (1.5 passes/km) that are suitable for dispersal of large mammals. This is also in compliance with Spanish regulation for motorways crossing through forested areas (1–2 passes/km). We did not study the forest stretch to the south of Lerma (fig. 1) because it is occupied by a golf course surrounded by a metallic fence with a concrete base that prevents colonization by terrestrial animals.

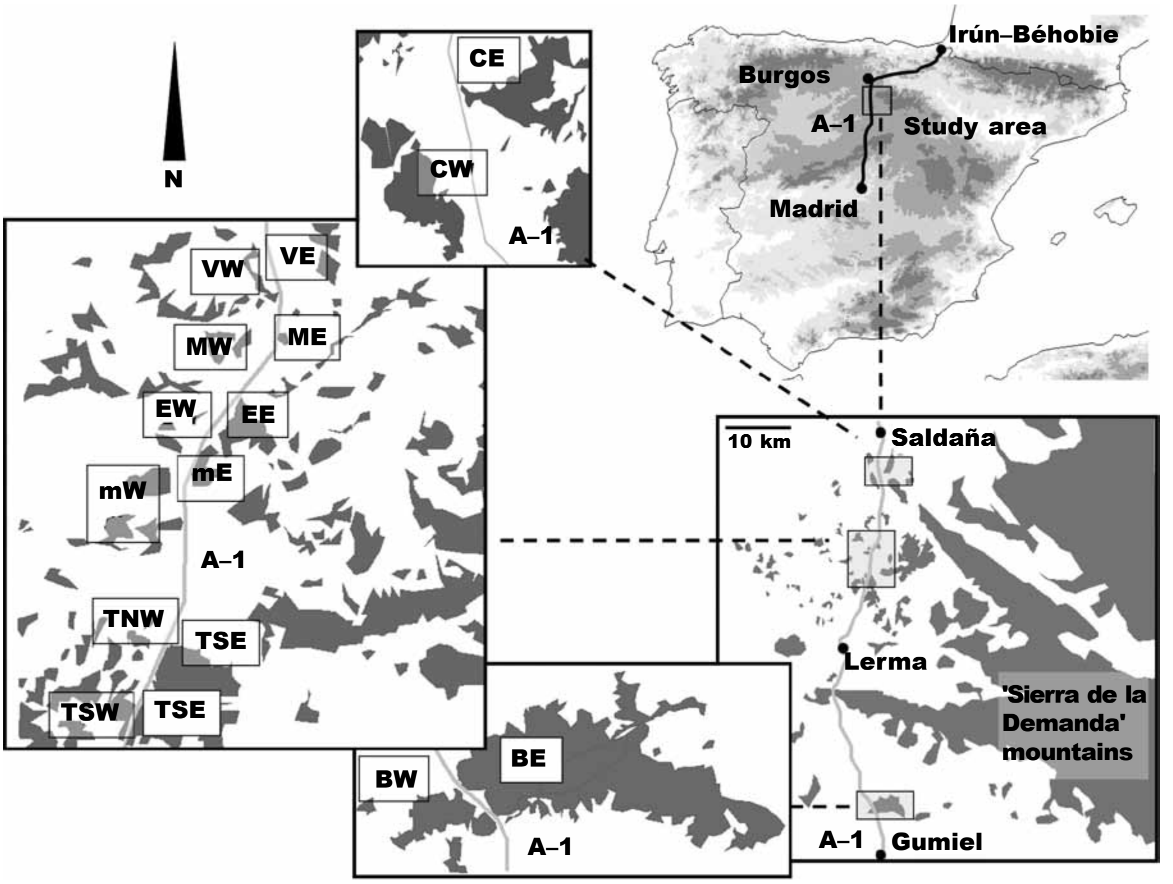

Fig. 1. Geographical location of the study area. The location of the A–1 motorway is traced on the Iberian peninsula in the upper–right panel, with the distribution of highlands and mountains (areas over 1,000 m a.s.l.) shown in a darker shade. The lower–right panel shows a general view of the study area. The three small squares represent the locations of study sites (magnified on the left). Codes refer to forest shown in table 2, with the E and W suffix differentiating eastern and western locations, respectively.

Fig. 1. Localización geográfica del area de estudio. En el panel superior derecho se encuentra el trazado de la autopista A–1 en la península ibérica, junto con la distribución de montañas y mesetas (zonas situadas a más de 1.000 m s.n.m.) en color más oscuro. El panel inferior de la derecha presenta una vista general del área de estudio. Los tres cuadrados pequeños representan la localización de las zonas de estudio (aumentados a la izquierda). Los códigos hacen referencia a los bosques de la tabla 2, con los sufijos E y W diferenciando las localizaciones oriental y occidental respectivamente.

Sampling protocol

We selected eight forest fragments as closely located to the motorway as possible on its western side, all of which had a contiguous forest fragment on the other side of the motorway (fig. 1). By selecting our fragments according to a paired design, we aimed to study differences in the occurrence and abundance of animals between forest fragments separated by the road. These fragments were more closely located to each other than any pair of fragments located on the same side of the road. We constrained our selection of sites to avoid fragments that were too small (< 1.5 ha) as patch size rather than isolation might determine occurrence of the studied species. However, the layout of fragment sizes and locations on either side of the road did not allow for a perfect design. Thus, we sometimes had to use adjacent fragments on the eastern side of the motorway to match western fragments suitable for our study (*e.g.,* the EE and mE sites in fig. 1, which are more closely located to each other than to their western counterparts). In one case (TNE and TSE sites in fig. 1), we had to use two study sites located on the same large fragment on the eastern side of the motorway. Nevertheless, these sites were more distantly located than some neighbouring forests in our study area, and could be considered to function as different sources of colonization of western fragments if dispersal westwards involved crossing the road.

We scored presence of vertebrates and measured their abundance in each study site from May to June 2009. We assessed the abundance of roe deer by counting faecal groups detected within a 1 + 1 m wide band (Tellería & Virgós, 1997) during the same time intervals dedicated to sampling lizards (see below). Abundance was estimated as the number of faecal groups/ha. Birds were counted early in the morning along 25 + 25 m wide transects and their abundance was estimated as number of birds/ha. Lizards were counted by means of time–controlled search. To prevent the confounding effects of circadian and/or weather induced variations in the activity levels of lizards (Díaz, 1991), two two–person teams connected by telephone simultaneously sampled the two fragments of each pair on either side of the motorway. Both teams started sampling at the same time, when meteorological conditions were appropriate for lizard activity. In each fragment, lizards were searched for during three person–hours, which was sufficient to detect the presence of the large psammodromus (mean ± SE time required to detect the first lizard was 12 ± 2.8', range 1–28'). Abundance was expressed as the number of lizards detected per 10' search. For eyed lizards, we only noted their presence/absence during the other species' counts, given their low densities and limited detectability (Díaz et al., 2006).

To control for possible confounding effects of features other than location of study sites with respect to the motorway, we measured the size of the fragments (which is a major determinant of vertebrate distribution in the study area) and their minimum distance to the motorway. These variables were estimated by means of the SIGPAC facility (http://sigpac.mapa.es/fega/visor/). We also examined vegetation structure as this can affect the distribution of forest vertebrates. We sampled habitat features within 25 m–radius circles evenly distributed along the itineraries used to census animals. In these plots, we visually estimated the cover of leaf litter, grass, shrubs < 2 m high, shrubs and trees > 2 m high, and deciduous oaks (*Quercus pyrenaica* and *Quercus faginea*). We also assessed the mean height of the tree canopy and the number of tree and shrub species. These variables were chosen because shrub and leaf litter are used as refuges by forest lizards (Díaz & Carrascal, 1991), the presence of deciduous oaks is related to more moist and more productive conditions in these Mediterranean forests, and the diversity of tree and shrub species has been related to the presence of roe deer, which require a variety of plant species to feed on (Virgós & Tellería, 1998).

Table 1. Results of principal components analysis of the variables measured to evaluate the vegetation structure of forest fragments. Figures show the factor loading of each variable on each component, the eigenvalues and the percentage of variance explained by each component. Significant factor loadings are shown in bold.

Tabla 1. Resultado del análisis de componentes principales de las variables medidas para evaluar la estructura de la vegetación de los fragmentos forestales. Las cifras muestran la saturación factorial de cada variable sobre cada componente, los valores propios y el porcentaje de varianza explicado para cada componente. Las saturaciones factoriales significativas se indican en negrita.

Variable	PC–1	PC–2
Cover of grass	–0.047	**0.831**
Cover of leaf litter	**0.725**	–0.272
Cover of shrubs < 2 m high	**0.564**	**–0.629**
Cover of shrubs and trees > 2 m-high	0.309	**0.675**
Cover of deciduous oaks	**0.809**	0.048
Number of shrub and tree species	**0.685**	-0.250
Height of the tree canopy	**0.819**	0.202
Eigenvalue	2.74	1.72
Explained variance (%)	39.07	24.56

Analyses

We used principal components analysis (PCA) to transform the variables of vegetation structure into a reduced set of independent components (table 1). PC–1 reflected a gradient of increased forest development, higher cover of leaf litter and deciduous oaks, and higher numbers of shrub and tree species. PC–2 represented a gradient of increased cover of grasslands with a scarcity of low shrubs. Factor scores of forest fragments on these gradients were used as surrogates of vegetation structure.

Differences in fragment occupancy between species and sides of the motorway were tested for significance using Fisher exact tests applied to 2x2 contingency tables. We used within–subjects ANOVA to analyse pairwise variation between eastern and western forests in the abundance of roe deer, birds, and large psammodromus, as well as in vegetation structure (as estimated by PC scores), fragment size, and distance to the motorway. Whenever it was necessary, variables were arcsine– or log–transformed to fulfil the requirements of parametric tests. All analyses were done with Statistica v7.1.

Results

Our study sites (table 2, fig. 2) were located at comparable distances from the motorway ($F_{1,7}$ = 1.99, P = 0.201) and showed similar vegetation structure on both sides of the motorway (PC1: $F_{1,7}$ = 0.03, P = 0.864; PC2: $F_{1,7}$ = 0.09, P = 0.763). However, the westward–directed ongoing forest fragmentation process made it impossible to find fragments of similar size on either side of the motorway (forest remnants were consistently

Table 2. Fragment size (area in ha), distance to the motorway (m), and abundance of four vertebrate species measured in study sites located on either side of the A–1 motorway (see text for details on the abundance indices used for each species: RD. Roe deer fecal groups/ha; LP. Number of large psammodromus/10'; ER. Number of European robins/ha; BW. Number of Bonelli's warblers/ha). Forests are presented from northernmost to southernmost, and codes shown in figure 1 are in brackets. ([a] Robins were contacted outside the census band).

Tabla 2. Tamaño de los fragmentos (área en ha), distancia a la autovía (m) y abundancia de las cuatro especies de vertebrados, medidas en las zonas de estudio situadas a ambos lados de la autovía A–1 (véase el texto para los detalles de los índices de abundancia utilizados para cada especie: RD. Grupos fecales de corzo/ha; LP. Número de lagartijas colilargas/10'; ER. Número de petirrojos/ha; BW. Número de mosquiteros papialbos/ha). Los bosques se presentan desde los más septentrionales a los más meridionales con los códigos de la figura 1 entre paréntesis. ([a] Se encontraron petirrojos fuera de la franja de censo.)

	Western study sites						Eastern study sites					
Forest	Area	D	RD	LP	ER	BW	Area	D	RD	LP	ER	BW
Cogollos (C)	79.4	180	0.0	0.0	0.24	0.24	100.3	300	0.0	0.0	0.29	0.43
Valdorros (V)	10.4	100	0.0	0.0	0.86	0.86	20.1	270	0.0	1.54	0.22	0.89
Madrigal del Monte (M)	2.9	400	0.0	0.0	0.0	1.79	1.7	10	16.7	2.17	0.0	2.94
Encinillas (E)	4.9	400	0.0	0.0	0.0	0.74	39.5	40	25.0	1.61	0.17	0.83
Madrigalejo (m)	22.7	200	0.0	0.0	0.47	0.94	18.6	50	14.3	1.22	0.0	0.86
Torrecilla del Monte N (TN)	8.0	100	17.9	0.0	0.0[a]	0.24	76.5	30	35.7	1.21	1.43	1.19
Torrecilla del Monte S (TS)	14.1	40	17.8	0.0	0.48	0.71	76.5	30	33.0	1.55	0.88	1.10
Bahabón de Esgueva (B)	48.6	40	0.0	0.83	0.0[a]	0.48	463.0	90	65.9	1.25	0.22	1.10

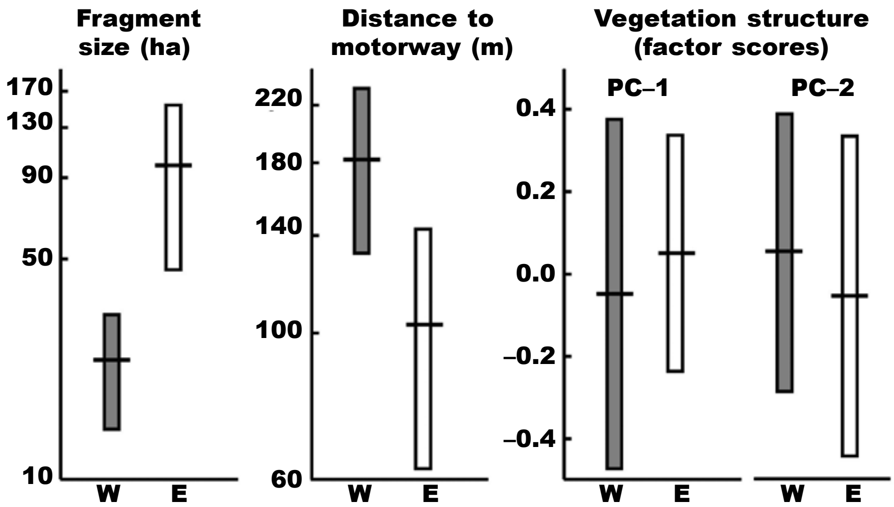

Fig. 2. Main features of the study fragments. Characteristics of the forest fragments studied on the western (W) and eastern (E) sides of the motorway (means ± 1 SE). The Y axes were plotted on log scale for fragment size and distance to the motorway to meet the assumptions of the analysis.

Fig. 2. Características principales de los fragmentos estudiados. Características de los fragmentos forestales estudiados en los lados occidental (W) y oriental (E) de la autovía (media ± DE). El eje de las ordenadas está a escala logarítmica, segun el tamaño del fragmento y la distancia a la autovía, para ajustarse a las suposiciones del análisis.

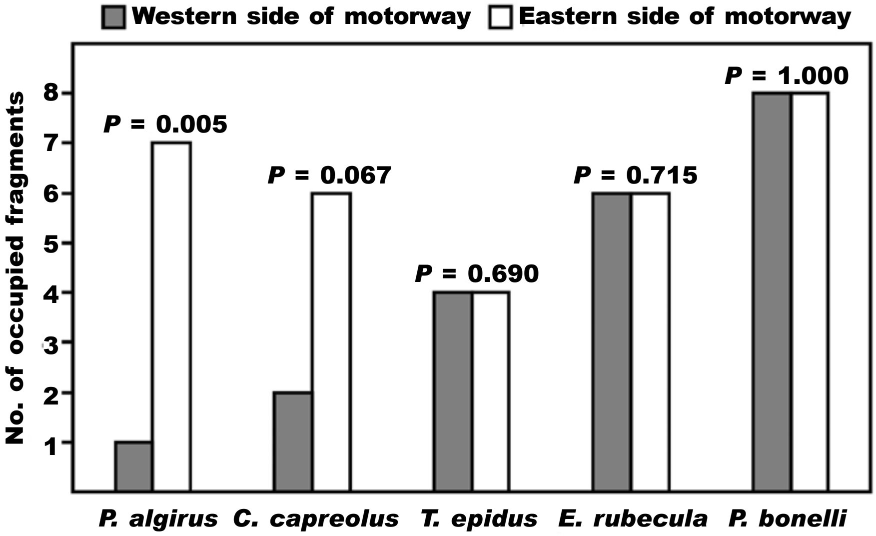

Fig. 3. Frequency of occupancy of forest fragments. Number of forest fragments occupied by each species of forest vertebrate on the western and eastern sides of the motorway. P–values indicate the results of Fisher exact tests.

Fig. 3. Frecuencia de ocupación de los fragmentos forestales. Número de fragmentos forestales ocupados por cada especie de vertebrado en los lados occidental y oriental de la autovía. Los valores P indican los resultados del test exacto de Fisher.

larger on the eastern side: $F_{1,7} = 6.74$, $P = 0.036$; figs. 1, 2). As a consequence, within–subjects ANOVAs with abundance indices as the dependent variable were re–analysed using the difference in fragment size between eastern and western sites as a covariate. Also, distance to the road was larger, though not significantly, on the western side. Thus, we included the difference in distance to the road between eastern and western sites as a second covariate.

A preliminary inspection of fragment occupancy on either side of the motorway revealed significant differences among our five model species (fig. 3, table 3). The large psammodromus and the roe deer were more frequent on eastern fragments than on western fragments (although the result was marginally non–significant in the case of the deer), whereas eyed lizards and birds occupied fragments with identical frequencies on both sides of the motorway (fig. 3). On the eastern side, where forest cover was higher and less fragmented, all but the most frequent species, Bonelli warbler, and the least frequent species, the eyed lizard, showed similar frequencies of occupancy (upper right half of table 3). However, on the western side, that had smaller and scarcer fragments interspersed among cereal fields (fig. 1), the large psammodromus occupied significantly fewer fragments than birds, with roe deer and eyed lizards showing intermediate frequencies between the large psammodromus and the birds (lower left half of table 3).

The numbers of animals on each side of the motorway also showed different patterns in the four species for which we could obtain accurate estimates of abundance (fig. 4). While psammodromus lizards ($F_{1,7} = 6.74$, $P = 0.002$), roe deer ($F_{1,7} = 9.37$, $P = 0.018$), and Bonelli's warblers ($F_{1,7} = 7.87$, $P = 0.026$) decreased abundance on the western side of the motorway, robins showed similar abundance on both sides ($F_{1,7} = 0.38$, $P = 0.559$). However, the difference vanished in the bird and the deer when fragment size and distance from the motorway were included as covariates in the within–subjects analyses (roe deer: $F_{1,5} = 3.44$, $P = 0.123$; Bonelli's warblers: $F_{1,5} = 0.74$, $P = 0.428$). On the other hand, the abundance of lizards was still lower on the western forests after controlling for the effects of covariates ($F_{1,5} = 18.99$, $P = 0.007$). Including vegetation variables (PC–1 and PC–2 scores) as covariates did not change the above results qualitatively (results not shown).

Discussion

An overview of the effects of the A–1 motorway on vertebrate distribution

A particular example of the negative consequences of roads for wildlife is the production of asymmetric effects on the surrounding landscape (Forman & Alexander, 1998; Taylor et al., 1993). Such an effect appears to be important in our study system where extensive eastern woodlands ('Sierra de la Demanda'; fig. 1) seem to operate as source areas for the

Table 3. Fisher exact tests comparing the frequency of occupancy of forest fragments by pairs of vertebrate species on the eastern (upper right half of the matrix) and western (lower left half) sides of the motorway.

Tabla 3. Test exacto de Fisher, comparando la frecuencia y la ocupación de los fragmentos forestales por pares de especies de vertebrados en los lados oriental (mitad superior derecha de la matriz) y occidental (mitad inferior izquierda) de la autovía.

	P. algirus	*T. lepidus*	*C. capreolus*	*E. rubecula*	*P. bonelli*
P. algirus	–	0.141	0.500	0.500	0.500
T. lepidus	0.141	–	0.304	0.304	0.039
C. capreolus	0.500	0.304	–	0.715	0.233
E. rubecula	0.020	0.304	0.067	–	0.233
P. bonelli	< 0.001	0.039	0.003	0.233	–

colonization of the fragmented landscape. Increased fragmentation westwards leads to a reduced cover of forests, which may reduce regional density of forest vertebrates around the motorway. As a consequence, and assuming a metapopulation dynamics scenario (Hanski, 1998), fragments on the western side of the motorway will have fewer opportunities to receive immigrants to compensate for local extinctions through a rescue effect (Brown & Kodric–Brown, 1977).

On the other hand, our design may be criticized because the present distribution of animals on the western side of the motorway should be compared with their distribution before the motorway was constructed, but we lack the data needed to perform such a comparison. This limits our ability to determine to what extent the observed distribution pattern is due to the motorway–caused interruption of the directional flow of individuals or to the reduced potential of

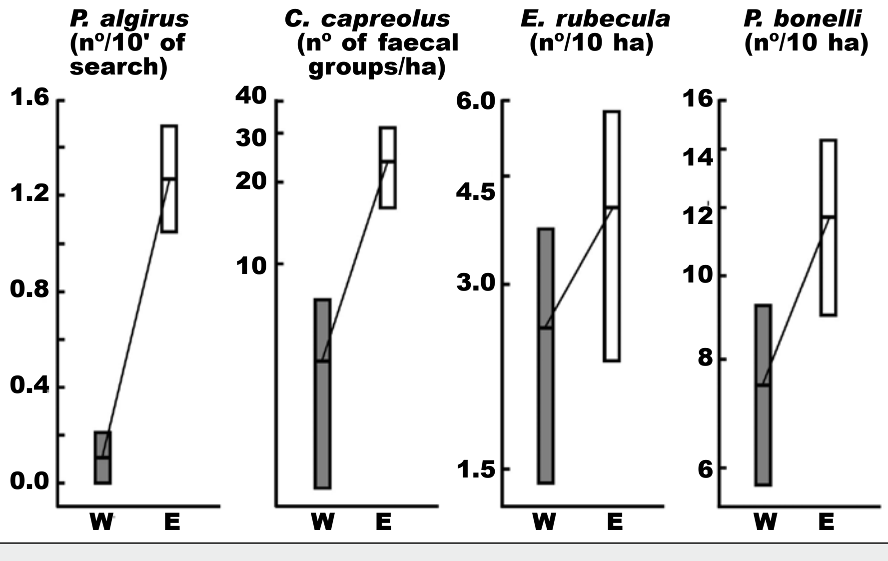

Fig. 4. Abundance patterns in forest fragments. Mean (± 1 SE) values of abundance indices computed for large psammodromus, roe deer, robins and Bonelli's warblers in forest fragments located on the western (W) and eastern (E) sides of the motorway. The Y axes were plotted on log scale when required to meet the assumptions of the analysis.

Fig. 4. Patrones de abundancia en los fragmentos forestales. Valores medios (± DE) de los índices de abundancia calculados para la lagartija colilarga, el corzo, el petirrojo y el mosquitero papialbo, en fragmentos forestales localizados en los lados occidental (W) y oriental (E) de la autovía. Las ordenadas se consignaron en valores logarítmicos cuando fue necesario, para ajustarse a las suposiciones del análisis.

the western forest archipelago to maintain metapopulations by autonomous extinction–recolonization dynamics. However, both processes predict population declines on the western side of the motorway, and they may even interact to produce synergistic effects. For instance, local or regional extinctions in disconnected western fragments will be difficult to avoid if animals coming from eastern woodlands are unable to cross the motorway. That the motorway hampers westwards dispersal was supported by the fact that isolated forests on the eastern edge of the motorway sustain populations of all studied species, while some of these species are absent or show reduced abundance in neighbouring forests on the western side of the road. Thus, the idea that reduced connectivity is responsible for the observed pattern seems to be supported by our data because, at the local scale of our study, landscape structure does not differ between eastern and western fragments (fig. 1). In fact, all study sites should be regarded as part of the same fragmented landscape (the distance between pairs of fragments ranges from 70 to less than 500 m; see table 2). As a consequence, we should not expect to find any difference between paired eastern and western fragments if the motorway, that provides the very basic criterion to divide the landscape into western and eastern sides, had not acted as a barrier that disrupts the westwards movement of individuals

Species–specific effects of the motorway

The distribution of species on either side of the motorway reveals lower frequencies of occurrence in western fragments for the large psammodromus and the roe deer (fig. 3). However, the other species occurred with exactly the same frequency on both sides of the motorway, although they differed in overall frequency of occurrence. The two bird species showed high frequencies of occurrence on both sides of the motorway (fig. 3), which was expected from their high dispersal capability. Besides, the abundance of bird species did not differ between the two sides of the motorway. We found a lower abundance of Bonelli's warblers on the western side, but the effect vanished when fragment size was included as a covariate in the analysis.

Eyed lizards had a scattered distribution, occurring in 50% of the fragments on both sides of the motorway. This result suggests that the distribution of eyed lizards is not affected by the motorway. In fact, compared to the large psammodromus, which is a forest specialist, the eyed lizard is a habitat generalist that can use a wide variety of habitats (uncultivated cropland boundaries, slopes or hedges) as corridors in cultivated landscape (Santos & Tellería, 1989). Moreover, eyed lizards are often found basking on road verges (in fact, road–killed eyed lizards are not uncommon in our study area). Such behaviour brings about opportunities for individuals to cross roads. However, further data (*e.g.* radiotracking, genetic analyses, etc.) is necessary to confirm that the motorway is unimportant as a barrier for the dispersal of eyed lizards.

Roe deer were broadly distributed on the eastern side of the motorway where they were only absent from the two northernmost forests, perhaps due to the disturbing effects of human activity generated in the nearby town of Burgos (population 180.000; *ca*. 10 km) and in three small villages in the close vicinity (< 1 km) of these forests. In contrast, on the western side roe deer occupied only the two forests located close to 'Torrecilla del Monte' (table 2, fig. 1). In this sector, the motorway is crossed by one overpass and five underpasses that are suitable for this species (protective fences running aside the motorway keep roe deer from crossing over the road). However, it is important to note that although the motorway might act as a barrier against the dispersal of roe deer, the distribution pattern of this species in the study area seems to respond mainly to fragmentation and habitat deterioration effects. In a study on the expansion of roe deer in central Spain, Virgós & Tellería (1998) showed that their need for large forests to rest and to browse was the main limiting factor. From this perspective, the western sector of the motorway offered less suitable habitat than the large forest patches on the eastern side, and in fact the difference in abundance between eastern and western remnants disappeared after controlling for the effects of fragment size. On the other hand, the Torrecilla sector, besides offering suitable underpasses, also retains a high forest cover on both sides of the motorway (fig. 1).

Finally, the large psammodromus offered the clearest example of the barrier effect caused by the motorway. This species was present in seven out of eight study sites on the eastern side, but only in one out of eight sites on the western side (fig. 2, table 2). Abundance was lower in western fragments, even after controlling for the effects of woodlot size and distance from the motorway. Previous studies suggest that the current size and habitat structure of forest fragments on the western side of the motorway make them suitable to host stable populations of these lizards (Santos et al., 2008); according to the logistic regression model used by these authors, the average probabilities of finding lizard populations in eastern and western fragments are 0.963 and 0.933, respectively, with no significant differences between the two sides of the motorway ($P = 0.380$). Therefore, it follows from our results that the large psammodromus faces a major barrier against dispersal, which has presumably stopped the westward expansion of the species. Moreover, a study of the distribution of the large psammodromus further to the west in our study area failed to detect populations in 17 forest fragments with suitable habitat for the species (Díaz et al., 2000). The absence of the species from the western part of this area was attributed to local extinction in forest remnants due to shrub cleaning produced by overgrazing and cultivation during the 1940s–1950s (Díaz et al., 2000). With the abandonment of such practice since the 1960s, forested patches have been regenerating in the study area, and we have found lizards in an increasing number of sites on the eastern side (Santos et al., 2008), an effect that has not been paralleled on the western side of the motorway.

Further research is needed to determine why the large psammodromus is so sensitive to the barrier effect, but some biological traits are candidate to explain its failure to cross the motorway. In the first place, the dispersal of this species through inhospitable habitat may be inhibited by its reluctance to move on bare ground. These lizards are positively associated with low shrub cover (Díaz & Carrascal, 1991) and they spend seasonal and daily periods of inactivity hidden in vegetated ground. Díaz (1992) showed that the choice of compass directions around oak shrubs allows sun–seeking lizards to minimize their escape distance towards the nearest shrub, thus reducing predation risk. It has also been shown that the approach and escape distances of lizards from a deciduous oak forest were larger at the times of year when oaks were unleaved (Martín & López, 1995). In the study area, although we have observed dispersal among nearby forest fragments across open fields (Santos et al., 2009), the species is rarely seen on bare ground. All these facts point towards the idea that the large psammodromus strictly avoids open surfaces such as paved roads and their ditches, which should make motorways formidable barriers for this species. Indeed, we have never found road–killed individuals of this species in our study area, although they are much more abundant on the eastern side of the motorway than eyed lizards.

Conclusions

Despite the well–known decline of animal populations in the proximity of linear infrastructures (Benítez–López et al., 2010), little work has been dedicated to explore the effects of roads on the spatial patterning of animal abundance. Although our study is geographically and taxonomically restricted, it supports the view that linear infrastructures are emerging determinants of the current configuration of species' ranges. Despite the efforts made to increase the effectiveness of crossing structures, many animal populations will face the detrimental effects of reduced population connectivity. This may produce decreased dispersal ability, delayed or suppressed re–colonization and, in situations of long–term isolation, extinctions and/or micro–evolutionary processes (Saccheri et al., 1998; Shepard et al., 2008; Strasburg, 2006).

In order to correct barrier effects caused by existing roads and highways and to prevent similar effects of the infrastructures to come, transportation planning and policy will require adding more proactive approaches to the already recommended construction of suitable passes. It will require monitoring the long–term effects of infrastructures on affected populations, and delineating specific management measures to preclude population decline or extinction. Options such as traffic management in some road sectors (*e.g.* traffic calming; Langevelde & Jaarsma, 2009), or translocation of individuals to reinforce isolated populations (Santos et al., 2009) appear to be suitable management approaches to prevent these negative effects on the distribution of terrestrial forest vertebrates.

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